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VOLUME XXXVII NUMBER 6

BOTANICAL GAZETTE

JUNE, 1904

CONTRIBUTIONS FROM THE CRYPTOGAMIC LABORATORY OF HARVARD UNIVERSITY. LVI.

NOTES ON THE MYXOBACTERIACEAE.

ROLAND THAXTER.

(WITH PLATES XXVI AND XXVII)

SINCE the appearance in this journal (June 1897) of the author's second paper on this group, comparatively little attention has been given to it, and with few exceptions one finds no mention of it in current text-books, or in bacteriological literature. Dr. Migula in his otherwise very complete *System der Bacterien* passes it with scant mention in his preliminary volume, and omits it wholly from the systematic part; where one finds such forms as Beggiatoa or Amoebobacter included in their proper connection. The *Pflanzenfamilien* also still appears to contain no mention of it, despite the inclusion of a menagerie of organisms whose zoology is orthodox to a degree.

In the second notice of the Myxobacteriaceae just referred to, mention was made of two papers by the late Dr. Zukal, in which he maintained the mycetozoan nature of these forms in connection with a new theory of the constitution of the myxomycetous plasmodium, based on his interpretation of the conditions seen by him in *Chondromyces crocatus*. In a third paper (Ber. Deutsch. Bot. Gesell. **15**: 542. 1897), however, he has discarded this opinion in favor of the writer's view of their nature, although still unable to abandon the idea that the gelatinous matrix associated with their vegetative condition may be protoplasmic. He further calls attention to the fact that *Myxobacter aureus* Thax. is synonymous with *Polyangium vitellinum* Lk., an organism which has at various times been looked upon as a gasteromycete, a myxomycete, and even as "insect eggs." He also describes as *Myxococcus macrosporus* n. sp. a form having spores 3 μ in diameter, and producing orange or flesh-colored pustules in a laboratory culture of moist bark. The figures which he gives in this connection are so evidently diagrammatic, however, that it is difficult to determine whether he was really dealing with a species of this genus. The appearances shown in *figs. 2* and *3*, and especially in *fig. 5* of his paper, are certainly not such as have ever been observed by the present writer.

A second addition to the order has been made by Miss A. L. Smith (Jour. of Bot. Feb. 1903), who has described as *Myxococcus pyriformis* n. sp. a short-stalked form found on rabbit dung from Wales; bright pinkish orange, about 250 μ high, and with spores 2 × 1.5 μ. Whether the pear-shaped cysts of this species are deliquescent or not is not stated. The cultures of dirty white motile rods obtained by transfers may certainly be assumed to have been impurities; since they do not appear to have had the characters which so clearly distinguish the vegetative conditions of the members of this group from that of other bacteria.

The third and last contribution that has appeared within the past six years was presented by Dr. E. Zederbauer at the May (1903) meeting of the Vienna Academy, and published in the proceedings (**112**: 447). In this paper, a considerable portion of which is devoted to an interpretative criticism of the two contributions which have been published in the GAZETTE, the author holds that the Myxobacteriaceae, as an independent order of organisms, has no real existence; and that the conditions supposed to have been observed merely represent a symbiotic association between ordinary Eubacteria and hyphomycetous molds. Since they are thus "no order of bacteria," this author, at the suggestion of Professor von Wettstein, proposes to designate them as "Spaltpilzflechten."

This treatment of the group, though novel, seems somewhat hasty; especially in view of the fact that the figures and descriptions given in this paper show very clearly that its author is as yet unacquainted with any member of the order he discusses, having been misled by fancied resemblances and influenced no doubt by an exaggerated notion of the difficulties associated with the differentiation of rod-like bacteria from Oedocephalum, Torula, and similar hyphomycetous types. A specimen of *Myxococcus incrustans* (*Torula Myxococci-incrustantis* n. sp. × *Bacterium Myxococci-incrustantis* n. sp.), which Dr. Zederbauer has kindly communicated to the writer, serves further to confirm this impression. An examination of this specimen shows it to consist of a horny incrustation which at least closely resembles a dried up mouldy plasmodium, blackened by the abundant fructifications of a toruloid hyphomycete; and from the fact that the bulk of the mass consists of calcic carbonate, one might perhaps venture the suggestion that it may be related to the Physareae. That a number of organisms are associated in this lichen can scarcely be disputed; yet whatever it may prove to be, either as a whole, or in detail, it surely has no connection with any of the Myxobacteriaceae, as this group is at present understood.[1] It seems, therefore, hardly necessary in the present connection to discuss the general characters of the order in the light of Dr. Zederbauer's conclusions; or to do more than reaffirm the account given in the writer's second paper, which is in his opinion substantially correct throughout.

The literary history of the Myxobacteriaceae thus bids fair to become as remarkable in its diversity as are the characters which make the order an anomaly among the plants which appear to be its nearest allies. There are certainly few groups including members which, as in the present instance, have been relegated to several genera of the Hyphomycetes, to the Gasteromycetes, to Eubacteria, to insect eggs, to Myxobacteria, to Myxomycetes, and finally to a group of "Splatpilzflechten;" and one can but look with no small interest, and perhaps with some misgivings, to such further taxonomic vicissitudes as may be in store for them.

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[1] Since the present paper was sent to the GAZETTE for publication a mounted preparation containing sections of authentic material of *Chondromyces glomeratus* has been received from Dr. Zederbauer and proves to be the conidial condition of *Coryne sarcoides* (Jacq.) Tul., to which the name *Tremella sarcoides* was given by Fries. It need hardly be remarked that this fungus is a widely distributed and very common form, well known to mycologists, having no connection either with "lichens" or Myxobacteriaceae.

Since the publication of his last paper, the writer has made no further detailed study of the group, having merely reexamined his preparations in order to assure himself that he had not been guilty of such blunders as were, perhaps unconsciously, attributed to him in Dr. Zederbauer's account. Although he has thus nothing new to add in relation to the general characteristics of the group as a whole, further careful study of these organisms is much needed, especially in connection with the movements of the rods and with their detailed cell characters. It seems by no means impossible that the pale pinkish coloring matter which appears to be invariably associated with the contents of the vegetative cells may be similar to bacteriopurpurin, and that these organisms may perhaps prove very near relatives of the Rhodobacteria; although there appears to be no indication of the presence of sulfur in the cell. It may be further remarked that the writer feels somewhat more inclined than formerly to entertain the suggestion, previously made, that these organisms may possibly represent transitional conditions between the higher bacteria and the lower Mycetozoa; having been partly influenced in this opinion by an examination of Dr. Olive's preparations of Diplophrys and the Sorophoreae, which seem to indicate that there may not be so wide a difference in cell structure between these groups as has been assumed.

Within the past few years a certain number of new forms has been accumulated, a majority of which are illustrated in the present contribution. In addition to these, two species of Chondromyces have also been met with; one of which was collected by Mr. A. F. Blakeslee on rotten wood in the Island of Margarita, Venezuela, and is allied to *C. crocatus*, although possessing a simple cystophore and differently shaped cysts; while the other, a somewhat amorphous species, was found on mosses growing on tree trunks at Intervale, N. H. Neither of these is available, however, in sufficient quantity for proper description. The species of Myxococcus are also certainly more numerous than the number of described forms would indicate; but as these need more careful examination and culture than it has been possible to give them, no additional species are here included; attention being merely called to the fact that a number of forms of the "rubescens" type, having spore masses of various colors, as, for example, magenta red, various shades of orange or yellow, milk-white, etc., should in all probability be eventually separated.

Among the new forms described below, *Chondromyces catenulatus* is a most interesting contribution to the group, since it presents a new type of cyst formation, and still further illustrates the remarkable resemblance which these pseudofructifications bear to the spores and sporophores of some of the higher *Fungi imperfecti*. As has been previously pointed out, the differences that are so marked in some of the species result largely from secondary impulses which, influencing the ultimate rod-masses at the period of cyst formation, produce in the mature cyst the distinctive form which in many cases is the most easily recognized and sometimes the only visible specific character. In *C. catenulatus* the conditions are unusually complicated for the reason that the ultimate rod-masses, having become more or less cylindrical, elongated, and sparingly branched,instead of responding to a single impulse in order to form a single ultimate cyst, is affected by a series of such impulses which cause the rods to stream together from opposite directions toward numerous successive points in the continuity of the mass; each point forming the nucleus of a distinct cyst. The ultimate masses thus become converted into chains of cysts united by slender isthmuses of variable length formed from the shriveled, tough, gelatinous secretions left behind by the moving rods (*figs. 3–4*), the whole pseudofructification thus assuming the form of a main axis or cystophore from the summit of which arise and diverge numerous series of spore-like cysts cohering in sparingly branched chains.

Of the three forms which have been referred to Polyangium, none corresponds very closely to the type, and the copious matrix of gelatinous material which surrounds the cysts in *P. vitellinum* is either wanting, or at least not as well differentiated. Of the new forms, *P. septatum* and *P. compositum* are both further peculiar from the secondary division of the primary cysts, of which the sori are composed, into a variable number of subequal portions clearly separated by straight lines of demarcation which give them a very spore-like appearance.

Chondromyces catenulatus, nov. sp. *Plate XXVI, figs. 1–5.*

Color bright yellow-orange. Cystophore simple, relatively rather short, the rather broad base spreading somewhat on the substratum, tapering to the distal end, where it is several times cleft; the divisions thus formed pointed, short, slightly swollen above the base and bearing one to several divergent chains of cysts. Cysts pale yellow, united in sparingly (once or twice) branched chains, fusiform to long elliptical, or often somewhat irregular in shape, the surface becoming more or less distinctly wrinkled at maturity, separated by longer or shorter, shriveled, membranous isthmuses; ten or twelve cysts often succeeding one another in a continuous series. Cystophore about 180–360μ in height. Cysts about 20–50 × 18μ, the longer chains 300μ. Average height of the pseudofructification 650μ. Rods 4–6 × 1–1.3μ.

On a rotten poplar log, Hanover, N. H.

This very interesting form was communicated to me by Professor G. R. Lyman, from whom I have received living material which, although it renews itself readily on the original substratum, I have been unable to cultivate on such media as I have tried. From the size of the spreading tuft of chains, often much more copiously developed than in *fig. 3*, it is a conspicuous species and is the only one thus far discovered with this peculiar cyst arrangement. The formation of the chain of cysts, which has been briefly referred to above, does not usually take place simultaneously throughout the ultimate rod-mass, but proceeds somewhat gradually from the base upward. As in other species, culture in a saturated atmosphere leads to the production of a variety of irregular and more or less abnormal forms, both in the cysts and in the cystophores, which tend to become short and stout.

Chondromyces pediculatus, nov. sp. *Plate XXVI, figs. 7–13.*

Orange-yellow becoming orange-red on drying. Cystophore solitary, erect, simple, usually rather slender and somewhat wrinkled; the cysts forming a loose, umbel-like head. Cysts pale yellowish, often nodding, nearly spherical to long-cylindrical, clavate or pyriform, usually broader and more or less abruptly flattened distally, where the papery cyst wall may be creased or folded so as to produce a more or less conspicuously roughened appearance; the base somewhat narrower, more or less wrinkled, passing with various degrees of abruptness to the pedicel, which is usually relatively long, slender, and shriveled. Cystophore about 300–700 μ in height, the head 150–500 μ in diameter. Cysts about 45–60 × 30–40 μ, their pedicels often 40–60 μ long. Rods of rising pseudoplasmodium 2–4 × 0.6–0.7 μ.

On goose dung from Sandy Run, S. C.

This species was first brought to my attention by my assistant, Mr. J. J. Wolfe, who found a few of its fructifications appearing on a laboratory culture. I have kept it in cultivation for more than a year and have thus been able to determine the constancy of the characters which seem to distinguish it very clearly from *C. crocatus*, or others of its nearest allies. In a saturated atmosphere its growth becomes very irregular, the cysts assuming a subcylindrical form, the portion of the ultimate rod-mass which is usually emptied to form the long pedicel encysting with little contraction, as shown in *figs. 6* and *11*. Under normal conditions, however, the peculiar form shown in *figs. 8, 9, 12*, and *13* appears to be very constant.

Chondromyces sessilis, nov. sp. *Plate XXVII, figs. 14–15.*

Reddish-orange. Cysts forming a sessile rosette or tuft on the substratum without any clearly differentiated cystophore; the individual cysts very variable in shape, irregularly broadly fusiform, often subapiculate, the surface somewhat wrinkled, very irregular in size, coherent at the base or more or less completely confluent into irregular masses. Cysts 18–55 × 25–75 μ, average about 40 × 55 μ. Diameter of rosettes about 100–250 μ.

On rotten wood near Miami, Florida.

This species was found in the hammock immediately south of Miami, and has the general appearance of *C. aurantiacus* to the naked eye. It is very irregular in its mode of growth, and specimens occasionally occur in which there seems to have been an attempt to differentiate an irregular cystophore. The rosettes can be removed *in toto* from the substratum, and when examined from the under side show the irregular area of insertion clearly differentiated from the cyst surface (*fig. 15*). Though often very variable and misshapen, the cysts are normally shaped like those shown in *fig. 14*, and always cohere.

Chondromyces muscorum, nov. sp. *Plate XXVII, figs. 16–18.*

Bright yellow-orange. Cysts simple or rarely furcate, sessile without any differentiated cystophore, erect, variously elongated;

stout or usually somewhat slender, tapering more or less prominently to the bluntly pointed apex. Cysts 90–300 × 20–50 μ. Rods 4–6 × 1–1.3 μ.

On hepatics on trunks of living beech trees, Crawfordsville, Indiana.

This species, which was kindly communicated by Dr. E. W. Olive, though unlike any other species of Chondromyces in general habit, is very similar in shape to some forms of *Myxococcus coralloides;* from which it differs, however, in its bright color, and more slender form, as well as by the absence of spores. It varies considerably in shape, from stout, bluntly rounded, to slender, more or less attenuated forms.

Myxococcus disciformis, nov. sp. *Plate XXVII, figs. 19–21.*

Cysts disk-shaped, crowded, sessile, attached by a more or less ragged scar-like insertion, or irregularly heaped in masses; at first faintly pinkish, becoming pale dull orange-yellow; circular to oval or somewhat irregular in outline; the cyst wall distinct, thin, becoming very slightly wrinkled. Cysts about 30–35 × 10 μ. Rods 2–3 × 0.5–0.6 μ. Spores irregularly spherical, hardly distinguishable in the tenacious matrix.

On muskrat dung from Stony Brook, Mass., and on deer dung from New Hampshire.

This well marked species, clearly distinguished by its color and disk-shaped cysts, has appeared twice on laboratory cultures, and is one of the most minute members of the group. At the period of cyst formation the rod often heap themselves in masses of varying size, and in these masses the cysts become differentiated by secondary aggregation somewhat as in Polyangium, so that many of them mature quite free from the substratum and thus lack the more or less characteristic scar corresponding to their insertion (*fig. 19, x*). In other cases the pseudoplasmodium appears to spread itself over certain areas of the substratum, which thus become powdered with a multitude of sessile cysts. The pale orange color is assumed only after the cysts are well matured, and seems due to a thin, papery, slightly wrinkled wall, within which the spores cohere in a matrix as tenacious as in the most characteristic cysts of Chondromyces, and in which it is only with great difficulty that the colorless rounded spores can be distinguished after crushing, even when examined with the highest objectives. Like *M. cruentus,* this species may thus be looked upon as representing a transitional condition between the Myxococcus and the Chondromyces types.

Polyangium septatum, nov. sp. *Plate XXVII, figs. 25–28.*

Sori yellowish-orange, becoming dull red-orange when dry, very variable in size, from fifty to several hundred μ in diameter, forming irregular, often variously confluent masses. Cysts irregularly rounded, subspherical to ovoid, irregularly angular or subcylindrical, divided into an irregular number of secondary cysts through clearly defined pseudosepta, the septation transverse or various. Cysts 18–22 × 12–22 μ. Secondary cysts about 10–12 μ. Rods 3–5 × 0.8–1 μ.

On horse dung, Cambridge, Mass.

This curious form has appeared twice in laboratory cultures, and is at once distinguished by its compound cysts, the septation of which is so regular and clearly defined that they have the appearance of fungus spores of the phragmosporic or dictyosporic type. The peculiarities of the species result, as is evident, from three successive aggregation impulses; first the general heaping up of the rod-mass, next the secondary aggregation of groups of rods within this mass to form the primary cysts, and lastly the ultimate aggregation of groups of individuals in these cyst masses by which they become divided into portions of considerable uniformity. The gelatinous matrix which holds the primary cysts loosely together is often scarcely distinguishable, and hardly to be compared to the well marked envelope of *P. vitellinum*. Although this as well as the following species differ in so marked a manner from the type, both in this respect and from the presence of compound cysts, it seems undesirable to separate these forms generically, especially in view of the fact that *P. sorediatum*, described below, appears in a manner to connect the two conditions.

Polyangium compositum, nov. sp. *Plate XXVII, figs. 29–30.*

Color dull yellowish-orange changing to dark red on drying. Sori irregularly scattered or loosely grouped on the surface of the substratum, consisting of one to several, rarely more than six, irregularly rounded primary cysts surrounded by a more or less distinct common gelatinous envelope. The primary cysts irregular in size, elliptical to irregularly rounded or variously lobed or elongated, divided into very numerous secondary cysts which are irregularly polygonal from pressure, and thin-walled, tending to become more or less evidently arranged in definite secondary groups within the primary cyst wall. Larger sori about 100 × 170 μ. Primary cysts 75 × 125–35 × 35 μ, average about 75 × 100 μ. Secondary cysts about 10–15 μ in diameter.

On rabbit dung from Sandy Run, S. C.

This peculiar form appeared on a somewhat old laboratory culture while the present paper was in preparation. It is very inconspicuous from its small size and dull color, as well as from the fact that the sori tend to become somewhat sunken in the viscous surface of the substratum. No rising rod-masses were obtained owing to the age of the culture, so that it was impossible to determine the dimensions of the rods. The general yellowish mucus envelope about the cysts is usually readily distinguished, and the primary cysts possess a sufficiently well-defined wall which in turn forms a common envelope about the thin-walled polygonal secondary cysts.

Polyangium sorediatum, nov. sp. *Plate XXVII, figs. 22–24.*

Sori dull orange-red, irregularly lobulated, the primary lobes usually forming more or less clearly distinguished irregularly rounded secondary lobules; the whole sorus consisting of a compact mass of small cysts, somewhat firmly coherent, the matrix forming a very thin scarcely distinguishable film about them. Cysts irregularly rounded, often somewhat polygonal from pressure, rarely double, the wall thick and clearly defined, their average diameter 6–7 μ, the smallest about 3 μ. Rods about 3–5 × 0.8 μ.

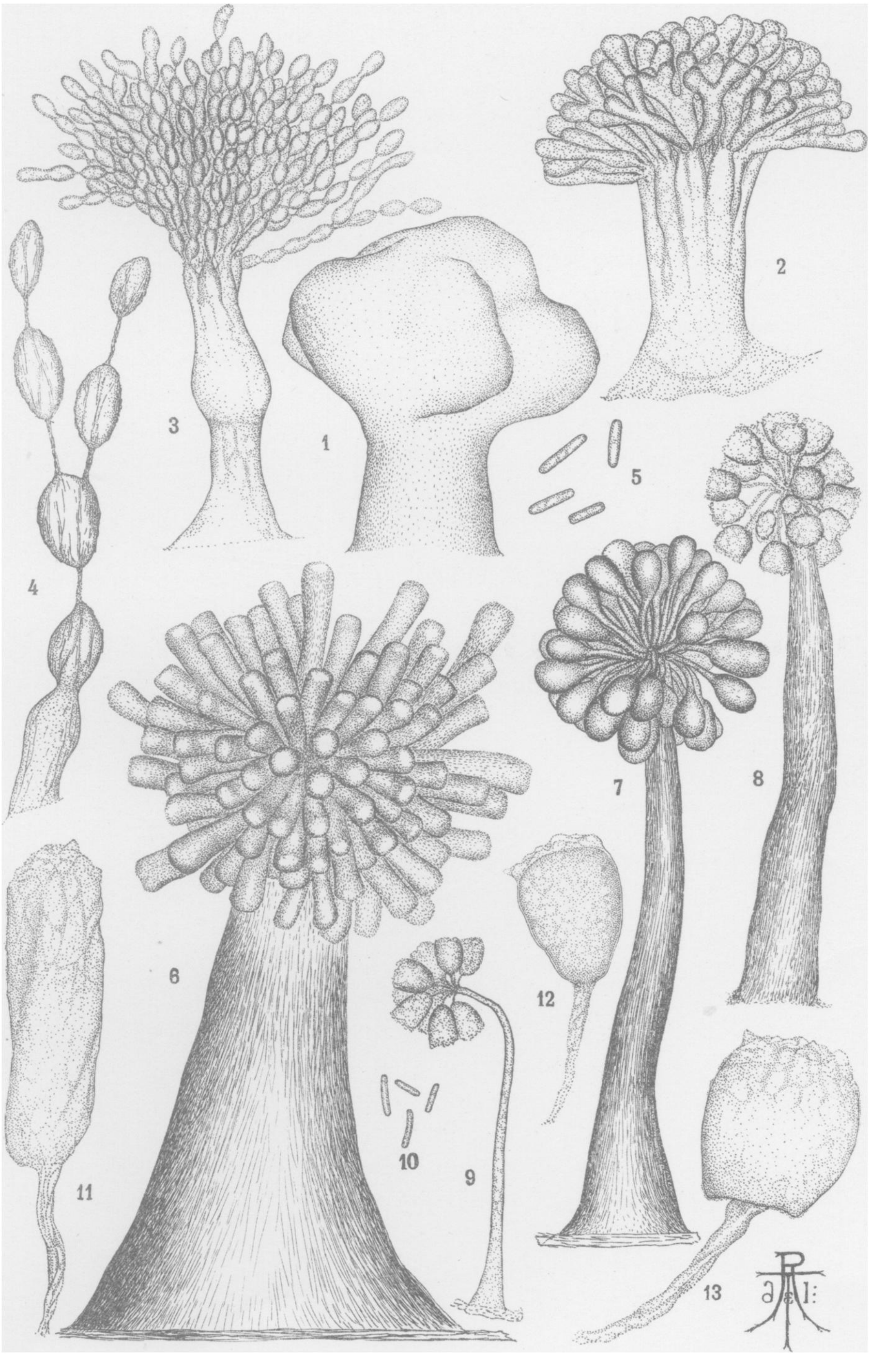
On rabbit dung from Sandy Run, S. C.

This species has been seen but once and in small quantity, attempts to cultivate it having failed. It is abundantly distinguished by its large sori and very minute cysts, which seem rarely divided in two, probably through accidental adherence.

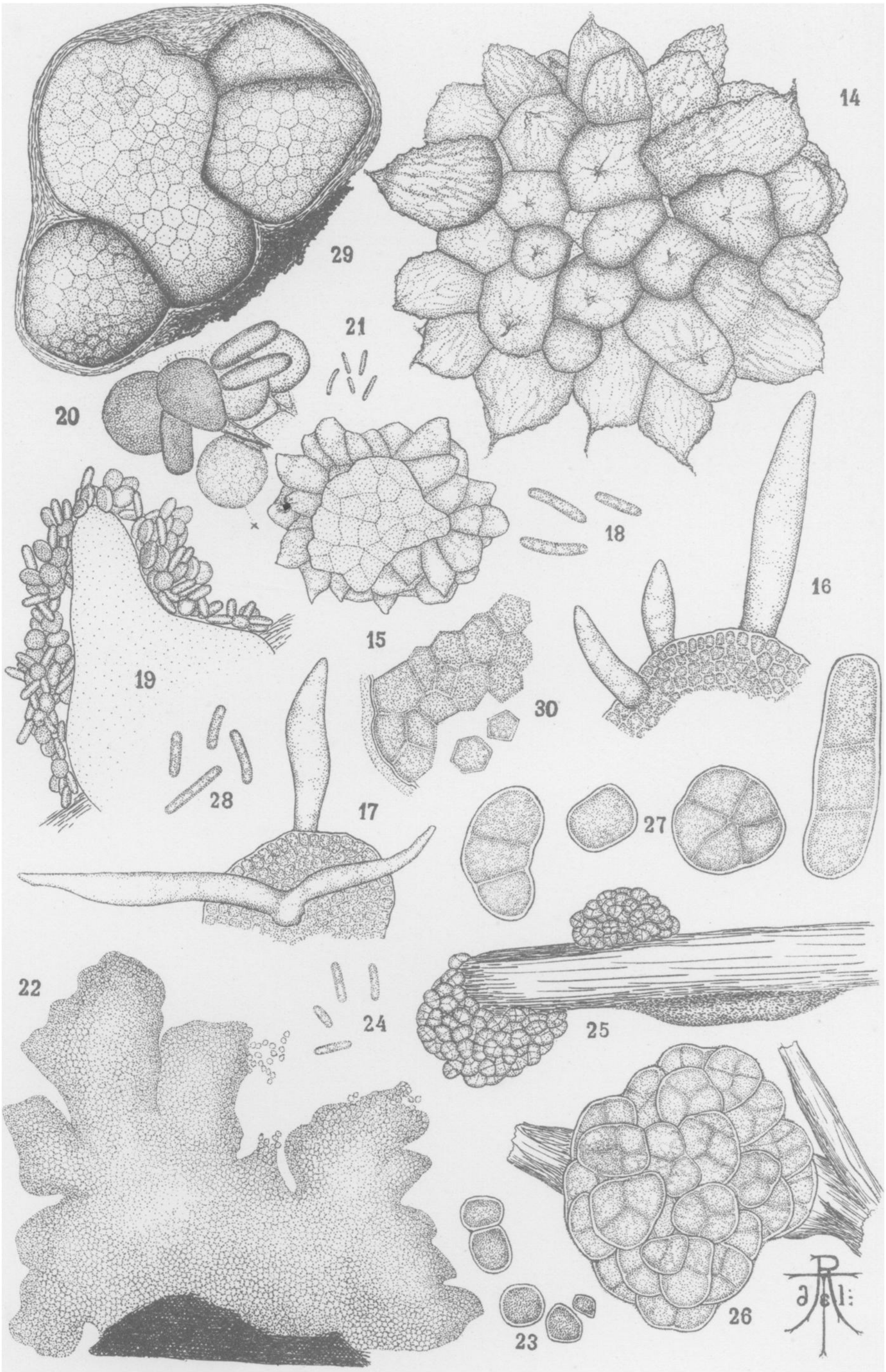
POLYANGIUM and CYSTOBACTER having proved synonymous, the former genus should include in addition to the above new species P. VITELLINUM Lk. (=C. aureus Thax.), **P. simplex** (Thax.) n. comb., and **P. fuscum** (Schröt.) n. comb. (=C. aureus Thax.).

CHONDROMYCES CROCATUS B. & C. has within the last few years been found at New Haven, Conn., by Professor Setchell; at Tabor, Iowa, by Professor H. Metcalf; and in Florida by myself; while Graf Solms Laubach (Bot. Zeit. **62**:39), in a criticism of Dr. Zederbauer's paper above mentioned, states that he found it on the fruit of Pandanus during his visit to Java.

CHONDROMYCES SACCHARI Speg. had been described in the *Revista de la Facultad de Agronomia y Veterinaria la Plata*, no. XVII, June 1896, but the description had not been seen when I published my last paper. The axis of this species is described as being formed "ex hyphis coalescentibus," although in the note following the description this statement is accompanied with



THAXTER on MYXOBACTERIACEAE.



THAXTER on MYXOBACTERIACEAE.

an interrogation. Except for its somewhat larger gross dimensions, this form, if really a Chondromyces, seems to correspond in all respects to *C. crocatus*, with which it is not compared by the author. Until further data are available concerning it, it is perhaps best omitted from an enumeration of the species of the group.

CHONDROMYCES AURANTIACUS (B. & C.) has been collected by the writer in Florida and received from the Philippine Islands, where it was found by Mr. Reade. This species is also reported from the environs of Vienna by Zukal.

CHONDROMYCES LICHENICOLUS Thaxter has been sent me on lichens from Crawfordsville, Indiana, by Dr. Olive, and I have myself found it growing on the algal scum covering wet boards of a mill race in Weston, Mass. Zukal also reports this species from Austria.

CHONDROMYCES SERPENS Thaxter is reported by Zukal from Austria, and I have myself recently found it again growing on an old dung culture.

CHONDROMYCES APICULATUS Thaxter, or what appeared at the time identical with this species, was found by me more than once during my stay in Florida a few years since, but as my preparations have been unfortunately lost or destroyed, I am unable to make sure of the accuracy of this determination. It has also been obtained on deer dung from the Philippine Islands.

EXPLANATION OF PLATES XXVI AND XXVII.

PLATE XXVI.—Chondromyces catenulatus Thaxter.

FIG. 1. Pseudoplasmodium rising to form pseudofructification. A + 4.

FIG. 2. A young pseudofructification in which the elongating ultimate rod-masses are beginning to branch before cyst formation. A + 4.

FIG. 3. An older stage in which cyst formation is almost completed. A + 4.

FIG. 4. A small chain of mature cysts. D + 4

FIG. 5. Rods from rising mass. Leitz $\frac{1}{16}$ oil + 4.

PLATE XXVI.—Chondromyces pediculatus Thaxter.

FIG. 6. Pseudofructification grown in saturated atmosphere, the subcylindrical cysts in process of formation. A + 4.

FIG. 7. Normal form in which cysts are forming, the cyst and pedicel already differentiated. A + 4.

Figs. 8, 9. Normal forms with cysts nearly mature. A + 4.

Fig. 10. Rods from rising mass. Leitz $\frac{1}{16}$ oil + 4.

Fig. 11. Somewhat elongated cysts with shorter pedicel. D + 4.

Figs. 12, 13. Normal cysts. D + 4.

PLATE XXVII.—Chondromyces sessilis Thaxter.

Fig. 14. Rosette of cysts seen from above. D + 4.

Fig. 15. Rosette seen from below. A + 4.

PLATE XXVII.—Chondromyces muscorum Thaxter.

Figs. 16, 17. Habit of mature cysts on hepatic leaves. A + 4.

Fig. 18. Rods of rising mass. Leitz $\frac{1}{16}$ oil + 4.

PLATE XXVII.—Myxococcus disciformis Thaxter.

Fig. 19. Group of cysts on Sphagnum leaf, two showing Myxococcus-like appearance of immature condition. D + 4.

Fig. 20. Masses of cysts formed on an old perithecium of Sordaria, the narrow ones seen edgewise. A + 4.

Fig. 21. Rods. Leitz $\frac{1}{16}$ oil + 4.

PLATE XXVII.—Polyangium sorediatum Thaxter.

Fig. 22. General habit of large cyst sorus. A + 4.

Fig. 23. Isolated cysts, two cohering. Apoch. water + 4.

Fig. 24. Rods in rising mass. Leitz $\frac{1}{16}$ + 4.

PLATE XXVII.—Polyangium septatum Thaxter.

Fig. 25. General habit of mature sori, with a rising rod-mass. A + 4.

Fig. 26. Small sorus enlarged. D + 4.

Fig. 27. Five cysts of various form. Apoch. water + 4.

Fig. 28. Rods from rising rod-mass. Leitz $\frac{1}{16}$ oil + 4.

PLATE XXVII.—Polyangium compositum Thaxter

Fig. 29. Sorus of four primary cysts. D + 2.

Fig. 30. Portion of margin of a broken primary cyst, showing secondary cysts, two of which are separate. D + 4.

Note.—The figures were drawn with camera, the combinations of eyepieces and objectives used being indicated in each case. Unless otherwise indicated, Zeiss objectives were used. The original drawings are reduced about one-fourth.